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Leaf Xeromorphy as Related to Physiological and Structural Influences..... LORA MANGUM SHIELDS 399

FUTURE CONTENTS
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THE BOTANICAL REVIEW

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LEAF XEROMORPHY AS RELATED TO PHYSIOLOGICAL AND STRUCTURAL INFLUENCES

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INTRODUCTION

The greater part of Maximov's masterpiece, The Plant in Relation to Water, based on original research and on more than 450 references, was ready for the press in 1925. While few investigators have recently considered the specific problems of drought resistance and xeromorphy, several significant contributions clarify earlier observations which were not understood 25 years ago. White's work on root pressure (1938) revealed why water moves in one direction through plant cells. Turrell's measurements of internally exposed leaf surface in xerophytes (1936) explained Maximov's observation that in the presence of adequate moisture transpiration is higher in xeromorphic than in mesomorphic leaves. Boon-Long (1941) interpreted the effect of high osmotic pressure in retarding water loss through decreasing cell permeability. Popp (1926), Shirley (1929) and Turrell (1940*a*, *b*) evaluated critically the influence of light intensity on leaf morphology. Wylie's studies of leaf structure in mesophytic and tropical dicotyledons (1939, 1943, 1946) suggest similar problems of transfer and contrasting surface-volume relationships in xeromorphic leaves. Mothes (1931, 1932) detected the effect of a nitrogen deficiency in contributing to xeromorphy. Other investigations of mineral nutrition have shown the effects of a deficiency or an excess of an element on water relations and structural modifications (Prianischnikov, 1928, 1935; Lundegardh, 1932; Hoagland and Broyer, 1943, *et al.*). Hoagland and Broyer (1936) determined the mechanism of absorption of these elements which so significantly affect the structure of many plant parts.

While no better explanation of survival in xerophytes is known than the one Maximov formulated, knowledge relating directly or indirectly to xeromorphy has been extended since his work.

STRUCTURAL MODIFICATIONS OF XEROMORPHIC LEAVES

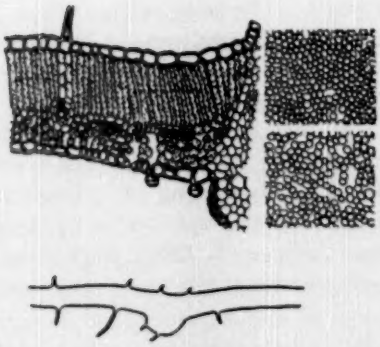
Xerophytes are dry habitat plants with transpiration decreased to a minimum under conditions of water deficiency (Maximov, 1931). Certain tissues of xerophytes, particularly those of the leaf, become altered structurally in relation to environment. The most obvious characteristic of xeromorphic leaves is the lower ratio of surface to volume (MacDougall and Penfound, 1928; Weaver and Clements, 1929) (Fig. 1). Reduced external area is accompanied by certain modifications in internal leaf structure: decreased cell size, thicker cell walls, a more compact network of veins, a higher stomatal frequency, and palisade strongly developed at the expense of spongy mesophyll (Schimper, 1903; Maximov, 1929; Weaver and Clements, 1929). Trichomes are also characteristic of many xeromorphic leaves, and water storage tissue forms in the xeromorphic succulent leaf type.

Certain of these modifications establish conditions favorable to increased photosynthesis and in many instances to increased transpiration as well (Maximov, 1931). Xerophytes, however, have in common an internal resistance which restricts water loss in time of drought and an ability to endure desiccation (Maximov, 1931).

The response of leaf morphology to external environment is recognized in the assumption that climatic agencies in areas having dissimilar vegetation can be compared through leaf-size groups constituting the flora (Raunkiaer, 1887).

ENVIRONMENTAL FACTORS WHICH CONTRIBUTE TO GENERAL LEAF XEROMORPHY

WATER DEFICIT. Leaf xeromorphy may result from excess transpiration or low absorption and the consequent water shortage which limits stretching growth (Schimper, 1890; Transeau, 1904). Cell walls thicken from accelerated conversion of polysaccharides into anhydrides or wall materials (MacDougal and Spoehr, 1918) deposited over the limited cell surface. Veins form a denser network, not being widely separated by laterally expanding epidermis



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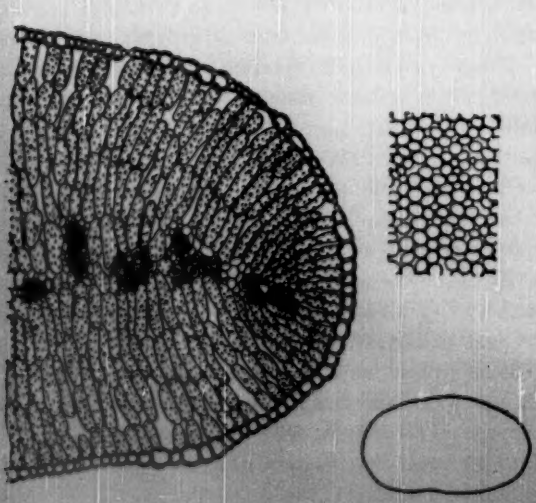

GREGGIA CAMPORUM LINEARIFOLIA

FIG. 1. Transverse and paradermal sections and trans-sectional diagrammatic outline of mesomorphic (above) and xeromorphic (below) leaf types. Note that while within a species cell size may be smaller in xeromorphic than in mesomorphic forms, leaf cells of xerophytic species are unusually large (Shields, 1951).

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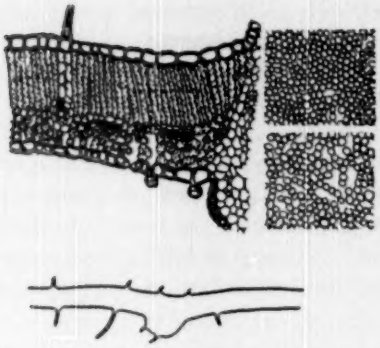

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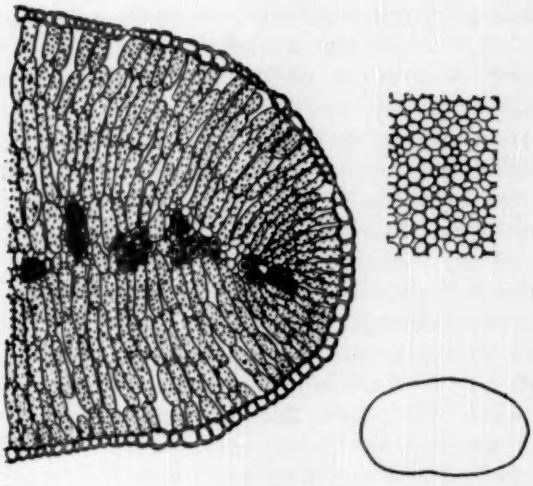

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and spongy mesophyll. The increased number of stomata per unit area results from limited enlargement of epidermal cells (Weaver and Clements, 1929). The plastic *Rumex acetosella* has one cell layer of palisade when grown under moist conditions, but when grown on dry sand two or three palisade layers form, and the leaves become thicker, smaller in size and revolute margined (Transeau, 1904). The amount of transpiration relative to water supply rather than absolute water loss leads to these structural modifications (Schimper, 1903), high evaporation influencing tissue proportions only when an internal water deficit exists (Cain, 1933).

HIGH LIGHT INTENSITY. Since the optimum light intensity for growth in leaf thickness is considerably higher than for increased surface, strongly illuminated leaves are small and thick (Schimper, 1903). Shade leaves of *Rhus toxicodendron* growing in moist dunes of a maple forest have five times the area of those from a sandy level with few trees (Turner, H., 1923), and compactness in spongy tissue varies directly with xerophily of habitat. *Vinca rosea* and *Nerium oleander* leaves are more xeromorphic when grown under 300-watt Mazda lamps than under similar 200-watt lamps (Turrell, 1940*a*). Twenty percent of summer sunlight favors maximum leaf expansion (Shirley, 1929), and above 50 percent ordinarily limits enlargement (Weaver and Clements, 1929). The optimum light intensity for the production of dry weight, however, increases with plant age (Combes, 1910). The percentage of dry matter in tops, the ratio of dry roots to dry shoots, density of growth and stem strength, as well as leaf thickness, increase with light intensity (Shirley, 1929). Plants grown in sunlight develop in the leaf mesophyll 77 percent more cell substance than do leaves of shade plants of the same species (Hormann, 1927). Large amounts of the blue end of the spectrum also induce xeromorphy, while removal of the blue portion, necessary for normal vigorous growth, stimulates mesomorphic development (Popp, 1926), but the decreased light intensity from removal of the blue fraction may contribute to this mesomorphy. Microphyllous plants as a rule are light demanding and succumb in competition with forest types if moisture conditions are sufficiently favorable (Thoday, 1931).

Light indirectly affects both transpiration and carbohydrate

synthesis. Depending upon the evaporating power of the air, the fraction of transpiration resulting from the direct effect of radiation varies from 38 to 81 percent (Martin, 1935). Since light intensity rises in advance of transpiration and of all other environmental factors and falls before transpiration or with it, radiation may be the primary causative factor in cyclic changes in water loss during the day (Briggs, 1916). The daily curves of cuticular transpiration in xerophytic *Rhododendron* and *Hedera* spp. follow the curve of light intensity more closely than the curve of water evaporation from an atmometer bulb (Mittmeyer, 1931). This is also true of total transpiration in sun leaves, possibly because the plant is more sensitive to light and an atmometer to wind (Maximov, 1929). Solar radiation is responsible for the great difference between day and night transpiration (Maximov, 1929). Even a 6.5-candlepower light accelerates water loss (Wiesner, 1877). Transpiration in *Hedera helix* and *Prunus laurocerasus* transferred from dark to light increases 30 percent (Darwin, 1914). Yet in 25 of 60 European plant species examined the stomata remained open at night (Stahl, 1919).

Transpiration is chiefly influenced by stomatal movement and soil water content (Maximov, 1929). Stomata of barley, wheat, oats and rye open in the light and close in the dark (Gray and Peirce, 1919). Stomata in species of *Poa, Festuca* and *Agrostis* open to a maximum from 9 to 10 A.M. and completely close at night (Carroll and Welton, 1937). Those of *Coffea arabica* remain open in dull weather or in shade, but in direct sunlight close between 10 A. M. and 4 P. M. from the action of light on the stomata and not from water relations of the leaves (Nutman, 1937). Stomatal behavior is such in eight trees and shrubs examined that the maximum standard rate of water loss occurs early in the day, usually between the hours of 8 and 10 A. M (Meyer, 1927).

Water availability influences the effect of light on transpiration. With adequate soil moisture transpiration in oaks is continuous during the day and ceases at night, but when soil moisture is near the wilting coefficient stomata may remain closed all day (Yocum, 1935). In castor bean soil moisture rather than light intensity conditions the ratio of average transpiration to xylem area (Penfound, 1932). The time of maximum opening of stomata on

citrus leaves is four hours after sunrise under moist conditions, but becomes progressively earlier as drought increases (Oppenheimer and Elze, 1941; Mendel, 1945). Stomata of xerophytes, however, close only in very intense light (Mittmeyer, 1931).

The role of light in regulating stomatal apertures may be controlled by variation in the hydrogen ion concentration of the guard cells which in turn governs turgor (Scarth, 1932). Light decreases acidity in the green guard cells, turgor is increased, and the stomates open (Scarth, 1932). Light may also affect permeability of the protoplasm in guard cells. Guard cells bounding closed stomata are filled with starch which changes to sugar as the stomate opens (Lloyd, 1908), the osmotic pressure rising simultaneously from 10 or 20 to 90 or 100 atmospheres (Iljin, 1914). Guard cells plasmolyze when a leaf is placed in salt solution, but regain turgidity as the salt penetrates, apparently inducing starch hydrolysis (Iljin, 1922). Transpiration in green areas of *Hedera* and *Pelargonium* leaves transferred from dark to light is double that in white leaf parts on the same plants (Leclerc du Sablon, 1913). In variegated leaves normally functional stomata may be entirely devoid of green plastids (Kummler, 1922).

There is also a non-stomatal control of transpiration from retardation of absorption, retreating of water menisci within the pores and diminishing pressure of water vapor at the cell surfaces (Maximov, 1929). Water, as well as dry matter, residual ash and potassium, in three to seven weeks old maize leaves increases in the early morning, falls to a minimum around 11 A. M., and rises again in the afternoon (Penston, 1938).

Increased light, decreased water or a combination of the two result in reduced leaf surface and greater leaf thickness (Clements, E., 1905). Upper leaves, farther removed from the water supply and exposed to higher light intensity, are more xeromorphic than lower leaves of the same plant (Zalenski, 1904; MacDougall and Penfound, 1928). Bright light and wind, however, are of secondary importance compared to deflection of the water current by transpiration of lower leaves (Maximov, 1929), limiting the water supply while upper leaves are still in the bud (Zalenski, 1904). The water content of successive leaves diminishes with increasing height to near the apical region, maximal water percentage being in the lowest leaves not past the

age of functional activity (Yapp and Mason, 1932). Increasing severity of conditions encountered in upward growth accelerates transpiration to the amount of 6.06 cc./m./day, to four meters in pine stands and 3.55 cc./m./day, to 6.1 meters, in aspen groves (Gates, 1926). While there is no constant relationship between cell length and stem length, in both tomatoes and zinnias the first ten cells behind the promeristem are shorter at successive stages in the plant's ontogeny (Bindloss, 1942), apparently from a diminishing water supply. As the position of the apple leaf approaches the shoot apex palisade cells become more elongate and compact and make up a greater percentage of the mesophyll (Cowart, 1936). In alfalfa the areas and internal-external surface ratios of primary, late primary, secondary, tertiary and quaternary leaves are, on the average, successively smaller (Turrell, 1942). Differences in thickness of leaves from the south periphery and center leaves on the same tree are usually greater than corresponding variations in leaves of mesophytic anad xerophytic forms of a species (Gates, 1917; Hanson, 1917). The pattern of foliar development in aster may be related to the concentration and distribution of auxin (Delisle, 1938), but these, in turn are influenced by water and light.

The minimal water content occurs in the sunflower leaf when one-third to two-thirds normal size (Yapp and Mason, 1932), water shortage at this critical stage apparently contributing to the changed anatomical elements in the ascending leaf series. In trees and shrubs, however, conditions of illumination and transpiration under which buds were formed the previous year appear to predetermine stomatal size and number, extent of conducting tissue and thickness of epidermal walls (Nordhausen, 1903). The number of mesophyll layers of a shade leaf probably is determined in the bud (Smith, 1934). Marginal dentation of *Riparia glabra* and *R. du lot* occurs before budding begins (Rodrigues, 1941). Yet, removal of lower buds of *Tilia europaea* causes the remaining one to develop abnormally large leaves, suggesting that the total cell number is not established at an early date (Ewart, 1906). The larger leaf, however, might result from increase in cell size rather than in cell number. In *Coldenia hispidissima*, cell number and arrangement are much the same in young and old leaves (Fig. 2), normal leaf enlargement consisting of increase in size

of existing cells (Shields, 1951). Removal of the inflorescence and axillary buds of tobacco causes an appreciable increase in leaf size on the upper one-third of the stalk with a proportional increase in size of epidermal aand palisade cells (Avery, 1934).

Modifications in sun leaves are attributed to a water deficit in tissues at some time during formation (Soding, 1934). When

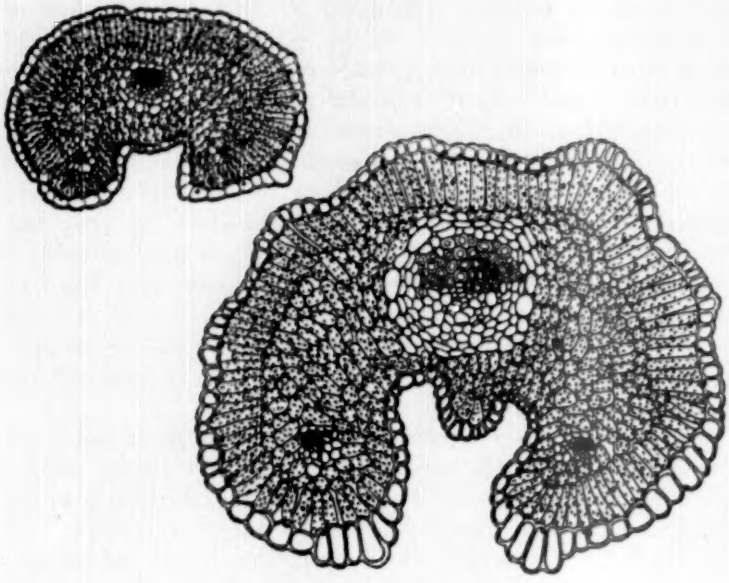


FIG. 2. Cell arrangement and cell number are much the same in young (left) and old leaves (right), enlargement consisting of increase in cell size rather than cell number (Shields, 1951).

Manihot utilissima is transplanted from a lighted place to shade narrow lobed leaves become broad lobed (Graner, 1942). Altering the availability of water by adding NaCl to the soil induces characteristics of sun leaves in all foliage of *Tilia cordata, Fraxinus excelsior* and *Acer platanoides* (Soding, 1934). Given an ample water supply, however, sun plants of *Helianthus* have larger leaves, larger epidermal cells, thicker mesophyll and more numer-

ous stomata than shade plants (Penfound, 1931). Mature shade leaves of *Cornus florida rubra* and *Acer platanoides* are smaller, as well as thinner, than comparable leaves from opposite unshaded shoots (Isanogle, 1944). Cell layers are the same in leaves having ten percent up to full intensity of sunlight, anatomical differences being the result of cell elongation (Isanogle, 1944).

The 15 taxonomic varieties of *Ranunculus scleratus* are believed to represent responses to different amounts of water (Folsom, 1918). It has been demonstrated in 200 genetically distinct groups that the same individual plant produces a more xeromorphic leaf type in alpine regions than in lowlands (Coulter, Barnes and Cowles, 1931). Xeromorphy in *Senecio* spp. in mountain ranges of equatorial Africa is correlated with altitudinal distribution of the individual species (Hare, 1941). No difference was observed, however, in size or anatomy of leaves and bud scales of *Populus tremuloides* collected at 5800′ and 9000′ in Colorado (Shope, 1927), probably because in this case moisture and temperature conditions were not more unfavorable at the higher altitude.

Ordinarily leaves of woody sprouts or saplings are larger than those of older trees, but certain young apricot trees were found to bear smaller leaves (Passecker, 1940). The average area of one blade surface for ten mature leaves from a cottonwood sapling five feet high growing in a calcium sulfate deposit was 18 square centimeters compared to a mean of 110 square centimeters in leaves of a nearby old cottonwood under equivalent conditions (Shields, 1951).

Increase in leaf blade area may accompany decreased surface tension of the leaf sap when energy gained as surface tension is reduced, accelerating chemical reactions on cell interfaces and resulting in increased area (Hercik, 1927). Possibly plant parts follow the compound interest law, the amount of material added in growth depending upon the amount already present (Blackman, 1919).

NITROGEN DEFICIENCY. In water cultures of *Nicotiana rustica*, *Zea mays*, *Coleus* and *Tradescantia albiflora* low nitrogen, as NH_4NO_3, induces xeromorphy, greater osmotic value and higher ash content percent of fresh weight, but less percent dry weight (Mothes, 1932). Low nitrate produces a relatively xeromorphic

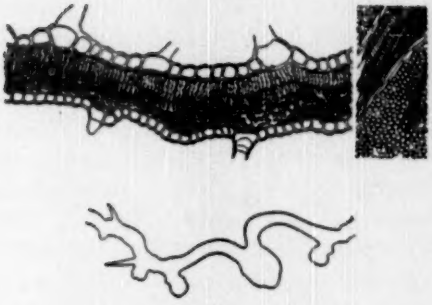
plant with thick cell walls, more mechanical and sclerenchymatous tissue, heavy cuticle and thick leaf epidermis (Kraus and Kraybill, 1918; Welton, 1928; Schneider, 1936). A high salt content is correlated with succulence, and high salt with low nitrogen produces a xeromorphic succulent leaf type (Mothes, 1932). Differences in the nitrogen supply and salt content may figure in the development of sun and shade leaves (Mothes, 1932). In wilted plants water and soluble nitrogen compounds are removed from older, lower leaves and transported into younger leaves at higher insertions (Mothes, 1931). Work with eight typical moor plants, however, indicates that xeromorphy results from a number of factors and not specifically from nitrogen starvation (Marthaler, 1939).

INFLUENCES RESPONSIBLE FOR THE GREATER DEVELOPMENT OF PALISADE

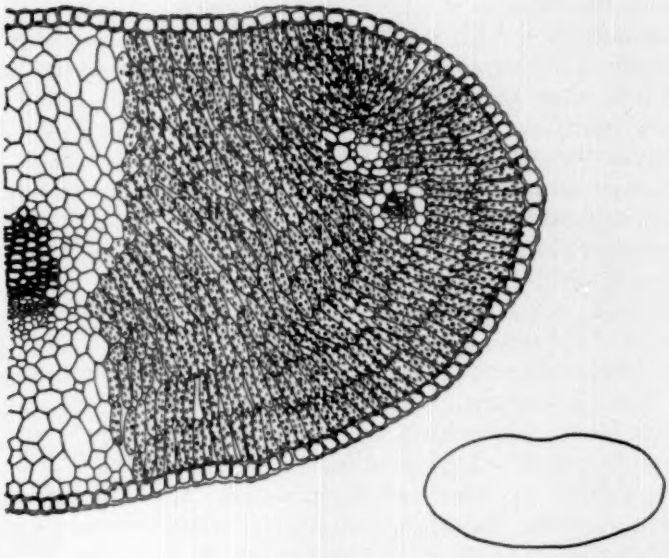
The increased thickness and smaller size of xeromorphic leaves are associated with the greater development of palisade, elongating vertically at the expense of laterally expanding spongy mesophyll (Fig. 3). High light intensity and an internal resistance to flow, resulting from a water deficit, apparently contribute to the formation of palisade tissue.

HIGH LIGHT INTENSITY. Intense illumination causes chloroplasts to aggregate into a compact clump, the majority in shaded positions, leaving the cell walls altogether (Frank, 1872) through passive transportation by the cytoplasm (Haberlandt, 1928). In weak or partially intercepted sunlight chloroplasts shift to the radial walls (Frank, 1872). The tension caused by laterally arranged chloroplasts may increase the horizontal cell axis at the expense of the vertical axis (Clements, E., 1905; Jost, 1907). This action of light on chloroplast arrangement and the consequent change in shape of cells containing them may influence leaf form, direct radiation causing chlorenchyma to elongate perpedicular to the surface (Weaver and Clements, 1929). Mechanical shock or injury, a water deficit, fluctuations in temperature or chemical stimulation, however, may also cause chloroplasts to shift from paradermal to radial walls and even to the center of the cell (Haberlandt, 1928).

Deeper palisade probably effects improved illumination of a



CUCURBITA FOETIDISSIMA



SENECIO SPARTIOIDES

FIG. 3. Transverse sections illustrating the contrasting combinations of volume and external surface in mesomorphic (above) and xeromorphic (below) leaves. In this *Cucurbita foetidissima* leaf, which exposed 282 sq. cm. of upper leaf surface and measured 150 μ from the upper through the lower epidermis, the surface-volume ratio was 133.2. In the *Senecio spartioides* leaf, exposing 4.65 sq. cm. total external surface and measuring approximately 1602 μ in thickness, the surface-volume ratio was 21.2 (Shields, 1951).

larger volume of cells (Thoday, 1931), but palisade is least developed in shade leaves most in need of light. Chloroplasts in palisade tissue behind a highly light diffusing epidermis are subjected to a light intensity which is directly proportional to cell diameter, narrow palisade protecting against intense illumination (Nielsen, 1940). Xeromorphic leaf structure in bog, heath and dune plants deficient in nitrogen may be an adaptation against too intense illumination of chloroplasts (Nielsen, 1940). In 19 of 37 plants with typical hereditary white mottling of the foliage, however, the classical palisade structure is present in the absence of chloroplasts (Conti, 1934). Palisade inception occurs independently of illumination in the darkness of the leaf bud, and most leaves, even in deepest shade, form some palisade (Haberlandt, 1928). Light intensity, however, apparently influences the location of this tissue most active in photosynthesis. In many leaves illuminated from both sides the entire mesophyll is composed of palisade, sometimes with a middle layer of intermediate cells. Palisade occasionally develops, however, immediately within the lower epidermis in shade leaves (Haberlandt, 1928). In *Iris japonica* leaves which normally have a palisade layer above and a spongy parenchyma below with stomata on the lower surface only, reversing the leaf position during development causes a reversal of tissues, but the effect of light on the dorsiventral condition is slight (Imamura, 1931).

Palisade is rare in stems which bear typical leaves. In certain species of *Polygala*, however, peripheral strata of stem cortex consists of palisade cells (Holm, 1929). In essentially leafless stems, as *Ephedra torreyana* (Fig. 4) and *Allenrolfea occidentalis*, deeper layers of stem parenchyma regularly elongate at right angles to the main axis, forming cortical palisade (Shields, 1951).

In English ivy starch accumulation under increased light conditions, and the subsequent conversion of starch to sugar, results in higher osmotic pressure and consequent cell elongation, forming palisade (Watson, 1942). In citrus leaves the ratio of depth of palisade tissue to leaf thickness is nearly constant for each of several species examined (Halma, 1929).

INTERNAL RESISTANCE TO FLOW. As water supply is depleted there develops a resistance to flow, accompanying a high osmotic pressure, which is the result of purely physical conditions in the

EPHEDRA TORREYANA

FIG. 4. Showing cortical palisade which often appears in essentially leafless stems.

plant and soil (Shreve, 1923; Emerson, 1947). Resistance to flow in the leaf is apparently greatest in passage through protoplasts of the mesophyll (Mer, 1940), and particularly from one cell to another (Maximov, 1929) rather than in minor veins. Yet when veins of *Ginkgo biloba* leaves are cut, water travels laterally through mesophyll cells with sufficient speed to maintain

life and rapidly enough to supply cells in certain cases to a distance of 2.6 mm. (Shull, 1934). In ivy leaves resistance to lateral flow is greatest in the spongy mesophyll (Ursprung, 1935). Intercellular spaces handicap diffusion through the mesophyll, and particularly the lateral discontinuity of palisade in mesomorphic leaves limits transfer through this zone in the plane of the blade (Wylie, 1943). The centric type of xeromorphic leaf, however, in which palisade cells radiate around central vascular bundles, reduces resistance in the mesophyll to a minimum (Thoday, 1931). Decreased internal resistance in xeromorphic leaves is more significant than reduction of external surface, which is often illusory (Thoday, 1931). Elongate palisade cells may facilitate transfer of food materials (Transeau, 1904), also, under the stress of a reduced water supply in xeromorphic leaves.

The relative volumes of sponge to palisade in groups of tropical and subtropical leaves yields a ratio usually related to mean vein spacing in the blade (Wylie, 1946). In mesophytic leaves increased amounts of palisade force veins closer together, while a larger proportion of spongy mesophyll favors their wider separation (Wylie, 1939). The average area of vein islets is smaller in leaves from older trees than in leaves from young trees (Tellefsen, 1922), which are ordinarily more mesomorphic in other respects as well. In xerophytes none of the veins are widely separated laterally, presumably because of limited expansion of sponge and epidermis in this plane (Weaver and Clements, 1929). A shift in the ratio of palisade to spongy mesophyll is automatically accompanied by an adjustment between vein frequency and size of intervascular areas. Since xeromorphic leaves are well vascularized, resistance to flow must originate outside the conducting system.

In *Acer pseudoplatanus* cambium in the leaf blade produces xylem only while the leaf is extending, no new veinlets developing after expansion ceases (Eliot, 1933), irrespective of changes in the environment which tend to deplete the water supply. In *Antirrhinum*, in contrast to the situation in *Crataegus* and *Solanum*, the genetic constitution of the epidermis apparently determines leaf form (Schiemann, 1940). The leaf epidermis of 46 mesomorphic species contains over 20 percent of the blade tissue and

seems to function in water conduction in areas between veins when closely connected with smaller veins by vein extensions which, for ten species, appeared along 58 percent of the total vein length (Wylie, 1943). Possibly epidermis influences leaf form, not only by lateral expansion, but also by supplying a significant fraction of total water. One stage in the growth of plum leaf buds is marked by stretching of the upper epidermal cells when the leaf flattens out, accompanied by continued division in the mesophyll. The frequency of cell division among palisade cells then becomes greater than in the spongy mesophyll, and the intercellular space system develops in this tissue as a result (Tetley, 1932).

Under conditions of water shortage *Rumex acetosella* forms drops of resin or oil in the epidermis and cells adjacent to bundles (Transeau, 1904), possibly inhibiting transfer. Xeromorphy in evergreens is correlated with resistance to flow by the wood, and plants in which conductivity is least impaired are least xeromorphic (Thoday, 1931). A water deficit stimulates production of not only palisade but also other elongate cells, including trichomes and root hairs (Yapp, 1912).

LEAF XEROMORPHY AS RELATED TO

WATER LOSS. Decreased leaf size, an almost universal modification in xerophytes, is commonly regarded as an adaptation which reduces transpiration. There is enough correlation between small-leaved plants and dry situations to lend color to this view, but shoots with pinoid, ericoid or cupressoid leaves are usually abundantly supplied with leaves, large numbers compensating for small size (Warming, 1925; Thoday, 1931). The total externally exposed leaf surface of certain conifers is often much greater than in dicotyledons, and north temperate Coniferae need and expend as much water as dicotylous trees (Groom, 1910).

The ratio of internal to external surface is low for shade leaves, equaling 6.8 to 9.9, and high for xeromorphic sun leaves, equaling 17.2 to 31.3 (Turrell, 1936). The greater internally exposed surface results from a more extensive development of palisade and is probably responsible, in part, for the transpiration rate in xerophytes (Turrell, 1936), which is high under normal con-

ditions (Schratz, 1931). The internal-external surface ratio is moderately but positively correlated with volume of the intercellular space (Turrell, 1940*b*).

Sun leaves of a variety of plants transpire more than shade leaves (Mittmeyer, 1931), often two to three times as much (Geneau de Lamarliere, 1892; Hasselbring, 1914). Shade plants of *Helianthus* and *Impatiens* transpire 50 percent less than sun plants (Meyer, W., 1934). In *Tilia*, *Acer* and *Ampelopsis* transpiration of sun leaves is greater than in shade leaves, both with and without water, and the degree of wilting of sun and shade leaves does not differ (Kisselew, 1927). In *Syringa* and *Caragana*, in which shade leaves wilt noticeably faster than sun leaves, transpiration of sun leaves is greater with a water supply and less without it (Kisselew, 1927). Sun leaves of the broad leaved evergreen *Olea europaea* transpire from three to ten times as much as shade leaves of the same species under normal conditions and two and one-half times as much as shade leaves under abnormal conditions (Bergen, 1904). Transpiration is neither negatively nor positively correlated with growth (Shantz, 1927).

In *Ipomea* leaves remaining after, or developing subsequent to, removal of leaves below them, stomatal equipment is significantly increased (Alexandrov and Alexandrova, 1927). There is no relation between the amount of transpiration and the number of stomata or length of the stomatal pore (Muenscher, 1915), but more numerous and smaller stomata tend to increase transpirational capacity (Yapp, 1912).

The absolute rate of transpiration at 6000′ does not differ from that at lower altitudes (Kochanovsky, 1926). Alpine plants appear to transpire on an average about as much water as those of the plains (Szmykiewicz, 1927), but data on transpiration at high altitudes are contradictory (Maximov, 1929).

TRANSLOCATION. Small leaves may offer better water economy in that all parts of the mesophyll lie within a short distance of veins (Thoday, 1931). In *Spiraea* the parts of leaf farthest from main channels of supply are the first to shrivel in drought (Yapp, 1912). Toward the tip a sunflower leaf withers more and sooner and recovers most tardily (Thoday, 1931). In lobed leaves the most vulnerable parts appear to be omitted (Thoday, 1931). The primitive angiosperm leaf was presumably lobed (Sinnott and

Bailey, 1915). Dicot leaves and leaflets with entire margins are predominantly in lowland-tropical regions; those with non-entire margins predominate in mesic cold-temperate areas (Bailey and Sinnott, 1916) where water is less readily available. Peripheral leaves of deciduous trees, as maple and elm, are more deeply lobed or more prominently toothed, as the case may be, and are smaller than leaves from the center of the same tree (Hanson, 1917). *Larrea tridentata*, the most successful and conspicuous xerophyte in North American deserts, produces prodigious numbers of bifoliate leaves believed to have been derived from a simple mesic ancestral leaf type (Runyon, 1934). Possibly in this case also the most vulnerable parts were omitted in adapting to xeric habitats. Given plenty of water, creosote bush behaves like an ordinary mesophyte (Spalding, 1904), but the leaf size and shape, not being plastic, do not change.

Anatomical differences in certain desert plants cannot account for differences in behavior (Shreve, 1923). Drought-resistant and partially expanded *Larrea tridentata* leaves which withstand a water content to dry weight ratio as low as 0.5 are anatomically similar to mature leaves on the same branch which cannot endure a moisture content much below a level characteristic of leaves of mesophytic woody plants (Runyon, 1936). This physiological difference is evidently related to conditions obtaining during the time the leaves are emerging from the bud (Runyon, 1936). A limited water supply increases drought resistance, evidenced by wilted buckwheat and sunflower plants contrasted with controls (Tumanov, 1927).

SHOOT-ROOT RATIO. In addition to transpiring surface, an estimate of total structural xerophytism must consider absorbing surface and resistance to flow from the root to the leaf (Thoday, 1931). Root systems may increase the water supply by more vigorous development or by deeper penetration of the soil (Iljin, 1916). Nineteen species under semi-arid conditions, however, developed fewer laterals than aquatic plants (Dittmer, 1948). High light intensity, which in most species causes diminution of stem and leaf size, accelerates root growth (Lubimenko, 1908). In sweet clover either cool temperature or a low moisture supply increases the proportion of total plant weight in the roots (Smith, T. J., 1942). The absorbing surface of corn, exclusive of root hairs,

amounts to 1.2 times the surface of above-ground parts in moist soil, and is 2.3 times as great in dry soil (Weaver, 1925), root area increasing as stem and leaf size diminish. Calcium causes a decrease in the shoot-root ratio of *Triticum vulgare* seedlings grown in single salt nutrient solutions (Kisser, 1927). Low nitrogen, as NH_4NO_3, reduces the shoot-root ratio in water cultures of *Nicotiana rustica, Coleus* and *Tradescantia albiflora* (Mothes, 1932). In barley and corn the greater ratio of tops to roots which results from increasing nitrate in the solution may be explained on the basis of increased use of carbohydrates in the tops (Turner, T. W., 1922) through protein formation in above-ground parts. The resulting decrease in the carbohydrate supply to the roots may bring about an absolute or relative reduction of root growth (Turner, T. W., 1922). Nitrogen deficiency in *Taraxacum kok-saghyz*, however, results in a far smaller fresh or dry weight yield of roots than do deficiences of phosphorus, calcium, magnesium or potassium (Meyer, 1945). The optimum concentration of sucrose for root growth in orchids is higher than the shoot optimum, the concentration which causes the greatest root growth suppressing growth of tops when introduced through the roots (Yates and Curtis, 1949). This suggests that the shoot to root ratio is a direct response to sugar concentration in the plant and that other factors which affect the ratio act through carbohydrate metabolism (Yates and Curtis, 1949).

Removing half the leaves of beet plants causes an increase in surface of those remaining so that the total leaf area of the plant remains constant (Kokin, 1930). Decreasing the number of leaves stimulates root development, however, one-third of the normal total leaf surface being sufficient to produce the usual root weight and sugar content (Kokin, 1930). The number of rings in beet root, however, is equal to one-sixth to one-third of the normal number of foliage leaves (Aleksandrov, 1929).

OSMOTIC PRESSURE. Higher cell sap pressure, resulting from a depleted water supply, increases suction power and decreases transpiration (Fitting, 1911), but absorbing forces of the cell wall rather than osmotic pressure may govern entrance of water (Livingston, 1911*a*, *b*; Briggs and Shantz, 1912 and 1913). The vapor pressure of a one molar solution, however, is only 1.8 percent less than that of pure water. Since the vapor pressure lower-

ing of the most concentrated leaf sap ever reported would not equal ten percent and vapor pressures of hydrated plant colloids are within two to five percent of those of pure water, neither osmotic concentration nor colloid hydration can account for drought resistance (Boon-Long, 1941). High osmotic concentration artificially induced by glucose injection, exposure to light or interruption of translocation, lowers tissue permeability to water, as tested by the plasmotic method (Boon-Long, 1941). Such decreasing of cell permeability to water by high osmotic concentration is largely responsible for the reduction in transpiration rates (Boon-Long, 1941).

Osmotic values of plant vacuoles in general range from three to 180 atmospheres (Zirkle, 1937). Relative osmotic pressures are indices of the ability of above-ground parts to compete for water (Herrick, 1933). Internal competition for water establishes consistently increasing gradients in the osmotic and suction tension values from lower to higher levels (Herrick, 1933), which accounts for internal translocation of water from lower to upper leaves during wilting (Pringsheim, 1906). In non-deciduous trees and shrubs cell sap density increases with height (Gail, 1926). Osmotic pressures in woody species are greater than in herbaceous plants (Korstian, 1924; Meyer, 1927), since herbs may not become modified physiologically for lifting water to such great heights as woody species. Osmotic pressures in leaves and internodes of *Ambrosia trifida* increase with age to a maximum, then decrease (Herrick, 1933). In *Larrea tridentata* the leaf water content normally increases with age (Runyon, 1936).

As a rule water is lower in leaves around mid-day because of the increase in photosynthate and other materials as well as from water loss, but *Larrea* and *Prosopis* may show a somewhat higher leaf moisture content by day than by night (Livingston and Brown, 1912). In *Ambrosia trifida* both osmotic and suction tension values tend to reach a daily maximum between 1:00 and 3:00 P.M. (Herrick, 1933). Reduced light causes a decrease in osmotic pressure of cell sap in both deciduous and non-deciduous trees (Gail, 1926), apparently through the effects of light on photosynthesis and transpiration.

Sun leaves of four woody prairie species have 1.1 to 11.6 percent lower water content than shade leaves and 2.1 to 5.4 atmos-

pheres higher osmotic pressure, the difference being explained by the higher transpiration rate in sun leaves (Marsh, 1941). Dwarf red kidney bean shows a progressive depletion of starch in leaves of plants permitted to approach wilting, while there is a marked build-up of starch reserves immediately following irrigation (Wadleigh, Gauch and Davies, 1943). Osmotic pressure is affected by interconversion of carbohydrate as well as by water loss directly.

Osmotic pressures of sclerophylls from arid regions are higher than in those from forest areas (Wood, 1934), the highest cell sap densities usually occurring on the most adverse sites and in more drought resistant species (Korstian, 1924). Chemical properties of the tissue fluids depend upon environmental factors and species peculiarities, and even in a mesic environment the xerophyte often has a higher osmotic pressure than mesophytes (Maximov, 1929). The range of cell sap concentration within a species, however, is regulated by external, not internal factors (Mallery, 1935). Cell sap concentration in deep-rooted prairie plants may increase 30 atmospheres as the soil dries (Stoddart, 1935).

Osmotic pressure in different parts of the leaf is closely related to the amount of available water (Iljin, 1916). Cell sap concentration is higher along the margin of wide leaves, measuring 0.64 atmosphere on the edge of a *Verbascum lychnitis* leaf and 0.43 atmosphere in the middle; osmotic pressure in the narrow leaves of *Saxifraga aizoon* measured 0.62 atmosphere, both in the middle and along the margin (Iljin, Nazarova and Ostrovskaja, 1916). Low osmotic pressure in leaves, identical with that of roots, occurs in plants thickly surrounded by a dense stand, osmotic pressure in *Poa pratensis* under these conditions measuring 0.37 atmosphere in both the root and leaf (Iljin, 1916).

Leaf compactness, in contrast to expansion, is associated largely with high relative transpiration, thus with high osmotic pressure (Coulter, Barnes and Cowles, 1931). The varying degree of cell sap density, acting on protoplasm, appears to be the stimulus and modified structure the effect (Schimper, 1903). Palisade, however, is usually best developed adjacent to the upper leaf surface through which less water is lost.

At higher altitudes *Caltha* has a greater amount of osmotically

active solutes (Montemartini, 1927). Yet investigation of 143 species shows that the ability of alpine plants to maintain themselves cannot be attributed to the high osmotic value of cell sap (Yoshi and Jimbo, 1931).

The osmotic pressure of *Larrea tridentata* root hairs known to function in absorption is ten atmospheres (Spalding, 1904). Certain older root hairs, which, from their regenerative capacity and action with plasmolyzing agents, also appear to be functional, have an osmotic pressure several times as high as young cells toward the root tip (Spalding, 1904). *Zea mays* absorbs throughout the entire root surface up to ten centimeters in length, but least is absorbed through the root cap, and less water enters through the zone of elongation than through older root parts (Hohn, 1934). As a rule, however, young root hairs have a higher equivalent (Hill, 1908). Root hairs are entirely absent from pecan (Woodroof and Woodroof, 1934) and are suberized in certain other species. The presence or absence of root hairs in *Zea mays* does not change the relative rates of absorption of the various regions in solution; yet it cannot be said that root hairs are of no importance in obtaining water from dry soil or in solute absorption (Hohn, 1934). *Triticum vulgare* seedlings grown in single salt nutrient absorb most in potassium solutions, although root hairs fail to appear, and water economy is least favorable in calcium solution in spite of well developed root systems with abundant root hairs (Kisser, 1927).

Apparently under conditions of reduced transpiration water moves by osmosis across the differentially permeable multicellular membrane formed by living root cortex (Kramer, 1932). Accumulation of water in the vessels may result in the development of a positive hydrostatic pressure or root pressure (Kramer, 1932). This pressure is responsible for exudation from excised roots (Grossenbacher, 1939; Biale, 1941). Such secretion is not retarded by an opposed pressure of 90 pounds per square inch, a force sufficient to raise water to a height of 200 feet (White, 1938).

Where water is abundant changes in the transpiration rate precede changes in absorption, water intake being determined by water loss (Kramer, 1937). Otherwise, available water limits transpiration (Spalding, 1904). The lag of absorption behind

transpiration may result from resistance in living root cells between the epidermis and xylem (Kramer, 1938). The rate of water intake through a sunflower stem attached to a vacuum pump is increased 83-fold by excising the roots (Kramer, 1938). Absorption in certain other plants not attached to a vacuum pump is temporarily increased ten-fold by removing roots held at 6° C. (Kramer, 1938). Absorption then falls to a rate of 2.5 times that prior to removal of the roots, and the attached wilted tops regain turgor within five minutes (Kramer, 1938). In five- and seven-year-old pines, spruce and oaks, transpiration in the first minutes after cutting increases 20–30 percent, possibly from removal of tension in the vessels, and returns to normal intensity only after five, ten or 20 minutes (Iwanoff, 1928). *Aristolochia sipho*, with an external surface 300 times that of a spherical *Echinocactus*, loses 6000 times as much water (Schimper, 1903), apparently because of a greater resistance to flow in the cactus and because its colloids resist dehydration.

Water is more readily absorbed through dead than through living roots, shown by a vacuum pump attached to a decapitated stem (Kramer, 1933). Plants with boiled roots, however, remain fresh no longer than stems severed under water (Watson, W., 1894), transpiration drops rapidly after roots are killed, and root pressure does not exist in dead roots (Kramer, 1932). Resistance to flow in the root, greater at low temperatures because of the increased viscosity of both water and protoplasm, may be the principal reason for inability of plants to absorb sufficient water at low temperatures (Kramer, 1938).

Surface reduction in small leaves may be incidental or even illusory, but internal resistance to movement of materials, resulting from high osmotic pressure, is apparently decreased by proximity to veins and by the greater amount of palisade characteristic of xeromorphic leaves, often arranged around a central vascular bundle, diminishing the number of membranes in each radius.

LEAF DURATION. Inefficiency of the conducting system appears to be one of the internal factors which limit the life of leaves and ultimately of plants, photosynthetic activity of a leaf terminating first in the marginal and intervascular regions (Dastur, 1925). Anthocyanin formation, which ordinarily precedes leaf fall, is apparently facilitated by interrupted translocation and sugar ac-

cumulation in the leaves (Griffin, 1935). Sugars, however, appear to be transferred from deciduous leaves into the branches or tree trunk before leaf fall, as sap expressed from freshly fallen leaves is more readily frozen than that from leaves shortly before abscission (Gail, 1926).

Factors that decrease photosynthetic activity are accompanied by increased leaf duration and thus by an increase in photosynthetic area (Pease, 1917). Leaf duration on evergreen trees and shrubs is shorter in the open than in the shade and shorter on the windward than on the leeward coast, factors favoring transpiration being accompanied by decreased leaf duration and reduced transpiring surface (Pease, 1917). In the Po Valley the last leaves to fall from the poplar are those at branch ends, transpiration in poplar being chiefly stomatal, and the young leaves, having more mobile stomata, control water loss better (Montemartini, 1930). The last mulberry leaves to fall are those at the branch base, transpiration in mulberry being chiefly cuticular, the older leaves being better protected (Montemartini, 1930). In the monsoon climate of India leaf fall is more frequently an indication that the plant is about to bloom than of drought (D'Almeida and Desai, 1942). In the uniform climate of Singapore, trees of a number of deciduous species change leaves annually, many in February, others in August, apparently because of leaf senescence (Holttum, 1931).

TEMPERATURE. Temperature affects the plant indirectly as one of the factors influencing the moisture deficit (Maximov, 1929). Both respirational and transpirational losses from the leaves increase progressively with each successively higher temperature where bean, milkweed and tomato plants are held in darkness overnight at 4°, 10°, 20° and 30° C. (Hewitt and Curtis, 1948). Transpiration in *Helianthus annuus* six to eight weeks old varies little with soil temperature between 55° and 100° F., but falls rapidly below 55° F., is reduced to half at 38° F., and approaches zero at 32° F. (Clements and Martin, 1934). Small leaves and leaves arranged parallel to incident light rays may be less rapidly heated by the sun. About 50 percent of the total radiant energy of the sun is transformed in the leaf and used in vaporizing water, more rapid in sun than in shade leaves (Marsh, 1941). Under

ordinary circumstances thermal emission accounts for more than 50 percent of the heat lost from leaves of *Liriodendron tulipifera* (Watson, 1934). Transpiration, higher in xeromorphic leaves, may at times prevent leaves normal to the sun from being injured, waxed apple leaves becoming 6° to 9° C. warmer than those which are transpiring (Wallace and Clum, 1938). There is no significant temperature difference, however, between waxed or blackened *Opuntia* pads and controls (Wallace and Clum, 1938). The cooling effect of transpiration is small compared with effects of light intensity, angle of incidence, convection, radiation and air currents (Clum, 1926*b*). The maximum difference observed between a transpiring leaf and air temperature in the open is 13.1° C. (Clum, 1926*a*). Leaf temperature seems to depend more on light intensity than on transpiration rate (Clum, 1926*b*). Changes in leaf temperature as great as 10° C. in one minute may be induced by natural or artificial changes in light intensity or in rates of air movement (Curtis, 1936). Conclusions of earlier workers that leaves in direct sunlight may be cooled by transpiration to below air temperature are questionable, since the methods used may give readings too high by 2° to 10° C., and leaves may be cooled 2° to 3° C. by radiation to thermocouples threaded into them (Curtis, 1936).

Increased temperature and higher relative atmospheric humidity cause leaf fall in rooted *Euphorbia pulcherrima* plants (Schnee, 1934). *Mathiola* has deeply notched leaves and no flower buds when kept at 60–70° F.; entire leaf margins and no flowers when maintained at 60–70° F. during the day and 50–60° F. during the night; and entire leaf margins and flowers when kept at 50–60° F. continuously (Post, 1936). While cooling impedes absorption and may lead to wilting in moist soil, young shoots of oats, barley and wheat continue to give off water when the soil temperature is nearly as low as 0° C. (Maximov, 1929). The root system develops better but more slowly at low temperatures (Maximov, 1929).

LIGHT QUALITY. Small leaves are exposed to a different quantity and quality of light. They are reached directly by rays containing all parts of the spectrum, not having been reflected from internal surfaces of other leaves (Thoday, 1931). Better develop-

ment, expressed in stem thickness and leaf size, is obtained in the full solar spectrum than in any portion of it (Popp, 1926; Pfeiffer, 1928). Poor growth under a forest canopy, however, is attributable to light intensity rather than light quality (Shirley, 1929).

CHLOROPHYLL CONTENT. Xerophytes have a higher rate of photosynthesis in spite of a decreased total chloroplast surface (Priestley, 1929; Thoday, 1931) and possibly paler chloroplasts, as where there is excess soil salt (Weaver and Clements, 1929). The sun leaf of *Taraxacum officinale*, however, is greener than the shade leaf (Gier and Burress, 1942). The chlorophyll concentration per unit area of internal surface is greater in high light intensity in the mesophytic *Vinca rosea*, but lower in the xerophytic *Nerium oleander* under the same conditions (Turrell, 1940*a*). Reducing light intensity to 12 percent of normal sunlight increases chlorophyll and carotinoids, but increasing duration of illumination decreases total chlorophyll (Guthrie, 1932). Chlorophyll concentration increases with decreasing light until the intensity is so low as to hazard survival (Shirley, 1929). The relative chlorophyll content in individual leaves of tropical plants varies with age, being low in young, highest in mature and declining in older leaves (Dastur and Buhariwalla, 1928).

The chlorophyll concentration in corn leaf tissue is not significantly correlated with yield (Miller and Johnson, 1938), but in *Ilex sugerokii leucoclada* the ratio of assimilative activity in one-, two- and three-year-old leaves is 1.00 : 1.53 : 0.87, respectively, and assimilation is positively correlated with chlorophyll content (Hiramatu, 1939). Intercellular space is significantly greater in basal apple leaves, but apical leaves, which are more xeromorphic, seem adapted to a higher CO_2 assimilation rate per unit of leaf area, due to the greater chlorophyll content and to the exposure of a larger internal cellular area per unit of leaf surface (Cowart, 1936). The palisade of normal apple leaves contains 85 percent or more, and spongy mesophyll 15 percent or less of the total internally exposed surface of apple leaves (Pickett and Birkeland, 1942). The extent of internally exposed area in apple leaves is evidently more important than chlorophyll content as a factor affecting photosynthetic activity (Pickett and Kensworthy, 1940). In mesomorphic leaves, however, palisade cells ordinarily contain

two to six times as many chloroplasts as in spongy parenchyma, and chlorophyll content is a fairly accurate criterion of photosynthetic capacity (Haberlandt, 1928).

ASSIMILATION. The greater internally exposed surface of xeromorphic leaves (Turrell, 1936) and the higher chloroplast content of palisade cells (Haberlandt, 1928) may explain in part their greater photosynthetic activity. Xerophytes produce more dry weight per unit of water used (Thoday, 1931), leaves assimilating more rapidly with low than with high moisture content (Dastur, 1925). The intensity of CO_2 assimilation in buckwheat and sunflower plants recovered from wilting is in some cases double that of unwilted controls (Tumanow, 1927). Measured in terms of CO_2 absorbed, photosynthesis is at a maximum in apple leaves whic have lost in drying 10–20 percent of their highest fresh weight (Alekseev, 1935). The greater stomatal frequency in xeromorphic leaves may facilitate the entry of carbon dioxide, accelerating photosynthesis (Thoday, 1931), though the stomatal openings are smaller, since the rate of gas diffusion does not decrease proportionately with reduction in aggregate pore area (Brown and Escombe, 1900). Closing of stomata at the beginning of wilting checks CO_2 metabolism (Maximov, 1929), but wilting is delayed in xerophytes. During the early part of the day photosynthesis may be correlated with light and later with transpiration, when water loss is closely related to the stomatal aperture, and under certain conditions photosynthesis is correlated with CO_2 concentration (Shirley, 1935). Under natural conditions low CO_2 limits assimilation and growth in wheat, flax and sugar cane (Singh and Lal, 1935).

Less leaf surface in sorghum is required to produce a bushel of grain in a dry than in a wet year, but the highest yields are obtained in seasons of abundant rainfall (Swanson, 1941). One plant, as sorghum or millet, may yield a pound of dry weight on one-third the amount of water required by another, as alfalfa (Briggs and Shantz, 1914). Drought resistance, expressed as ratio of dry substance accumulated per kilogram of water transpired, equals 1 : 300 in certain central European plants, including barley, oats and clover (Hellriegel, 1883).

MINERAL BALANCE. Total ash and nitrogen content are greater in plants grown in dry than in moist soils (Rippel, 1919), and

desert soils, in consequence of low leaching, are high in soluble salt. Under conditions of high transpiration plants may accumulate more ash, calcium, phosphorus and potassium as well as dry weight, intake of certain ions increasing with absorption, but not necessarily in proportion, and the rate for each ion varies with the kind of plant (Freeland, 1936). The amount of mineral intake is not proportional to either transpiration or water absorption. Salt accumulates in living cells against the concentration gradient by metabolic activity reflected in aerobic respiration (Hoagland and Broyer, 1936). Maize roots absorb NO_3 and PO_4 most rapidly after sunset, that time in the 24-hour period when respiration of the root system is most intense (Potapov and Stankov, 1934). During the day absorption is considerably less than at night (Potapov and Stankov, 1934). Decreasing transpiration of barley by half through increasing humidity or concentration of the nutrient solution reduces the ash content slightly (Muenscher, 1922). Decreasing transpiration by shading reduces photosynthesis and available food, and the ash content is correspondingly reduced (Muenscher, 1922). Ash content decreases from lower to higher levels in tree leaves (Seiden, 1926).

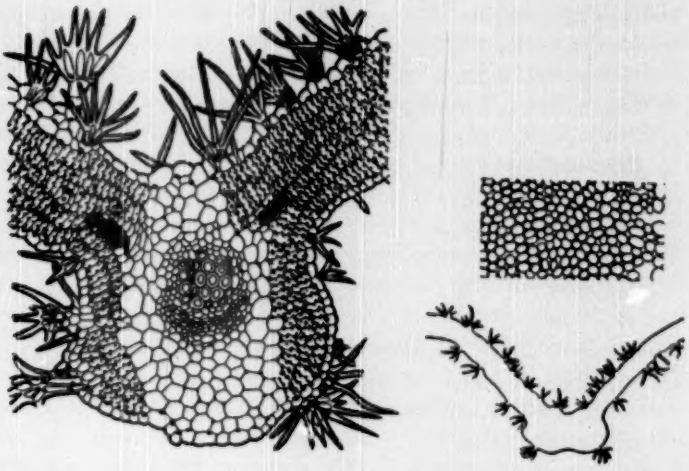
In barley the influence of light and humidity on transpiration are less apparent where roots have a high potentiality for salt absorption (low salt, high sugar status) than in those initially higher in salt (Broyer and Hoagland, 1943). Stomata of *Zea*, *Pisum*, *Phaseolus*, *Nicotiana* and *Tradescantia* respond sluggishly to environmental factors as a result of a nitrogen, phosphorus or potassium deficiency, accompanied by increased water requirement, decreased fruit yield, smaller plant size and a lower shoot-root ratio (Desai, 1937). Nitrogen deficient oat leaves are more active photosynthetically than those of comparable plants supplied with nitrate (Lundegardh, 1932). A phosphorus deficiency in *Hordeum distichum nutans* var. *kenia*, however, reduces photosynthetic activity by half (Muller, 1945). Senescence in potato leaves is delayed by adding moderate amounts of potash (K_2SO_4) to the soil, suggesting that pqtassium ions increase the catalytic activity of protoplasm (James, 1930). Under conditions of nitrogen deficiency there is a definite migration of nitrogen from relatively mature or senescent tissues to meristematic zones (Mason and Maskell, 1934). Directly or indirectly, it is probably assimila-

tion rather than absorption of nitrate which ordinarily limits growth (Nightingale, 1937; Davidson and Shive, 1934 and 1935).

Diminishing calcium is unfavorable to growth of sugar beets in ammonium cultures (Prianischnikov, 1928), while seedlings, as oats, barley and maize, relatively high in carbohydrate, and pumpkin, containing reserve fats, absorb ammonium rapidly from solutions containing ammonium sulfate or chloride (Prianischnikov, 1928). The pH and calcium content of the solution influence the relative absorption of ammonium and nitrate more than the stage of plant development (Prianischnikov, 1927, 1935). Root hair production is dependent upon an adequate supply of calcium (Farr, 1927; Loehwing, 1928), but calcium tends to accelerate transpiration (Chancerl, 1914; Hansteen-Cranner, 1914).

TRICHOMES

Trichomes are most abundant in xerophytes (Fig. 5), being in part responsible for the grayish aspect of desert vegetation. The shape and structure of trichomes are inherent, external factors determining only their presence or absence (Yapp, 1912). Where a single species exists as a mesophytic and xerophytic form, the latter is more hairy (Coulter, Barnes and Cowles, 1931). In certain plants drought increases the density of the hairy covering (Vesque, 1881), dryness stimulating the development of trichomes as it does of root hairs (Yapp, 1912). Hairy and smooth leaved plants of *Coreopsis lanceolata*, however, occur in the same habitat, and hairy and glabrous parts appear on the same *Polygonum amphibium* at the water's edge (Coulter, Barnes and Cowles, 1931). Pubescence is more apparent in upper leaves, which are more xeromorphic, and distribution of trichomes in partially hairy *Spiraea ulmaria* leaflets corresponds to localization of withering due to wind, marginal hairs being continuous with additional bands extending inward between main veins (Yapp, 1912). Possibly water inhibits hair development, as a damp atmosphere prevents development of thorns in *Berberis* (Lothelier, 1893; Goebel, 1898). Transpiration apparently acts as a releasing stimulus. There are no hairs in the leaf bud of *Spiraea ulmaria*, but pubescence develops and increases as leaves unfold, appearing first



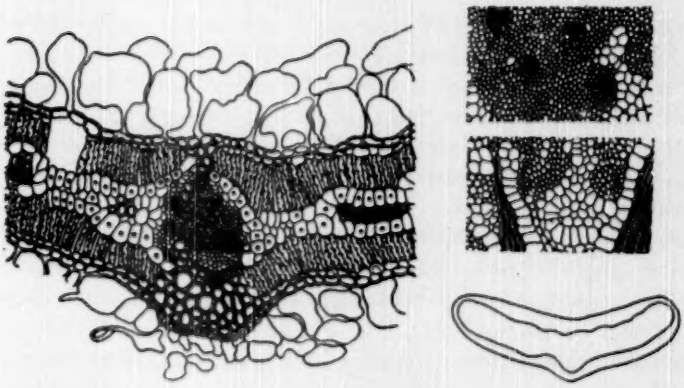


FIG. 5. Showing the stellate (above) and inflated balloon-like (below) trichomes on two xeromorphic leaf types (Shields, 1951).

along larger veins (Yapp, 1912). The initial stimulus appears to be fluctuating turgor in hair-producing cells (Yapp, 1912). *Spiraea ulmaria*, many other marsh plants and certain land plants exhibit a seasonal periodicity in hair production, a succession of glabrous, partially hairy and completely hairy leaves being followed by glabrous leaves in autumn (Yapp, 1912). Strigose hairs probably function mainly while organs are young, being denser at this time and becoming scattered as the surface increases (Coville, 1893). Hairs on unfolding leaves and growing shoots retard transpiration during windy and sunny times in spring before cuticle is fully developed (Kerner and Oliver). The trichomes on foliage of *Tussilago farfara* are effective only in wind (Brewig, 1933), stomata being exposed to suction in the wind so that gas exchange involves not only diffusion, but also the effect of moving air (Netolitzky, 1926).

Insect galls on smooth leaved species of *Vitis* are covered with a hairy coat, possibly because gall insects introduce osmotically active substances exerting an action on the leaf comparable to a xeric environment (Coulter, Barnes and Cowles, 1931). In swellings at the bases of glandular hairs of *Giardinia zeylanica* and similar cells of Vitaceae and Chenopodiaceae species potassium, associated with chlorine or carbonate anions, accumulates to the exclusion of any other cation (Lukaszewicz, 1926). Potassium salts increase osmotic pressure (Garner, McMurty, Bacon and Moss, 1923). Accumulation of KCl in these epidermal cells results from rapid transpiration (Lukaszewicz, 1926), and the resulting relatively high osmotic pressure may induce the formation of these swollen structures.

The effect of water shortage in producing outgrowths is also apparent where drought changes the branching habit of *Larrea tridentata* from one branch at a node to an opposite or whorled arrangement (Runyon, 1934).

No variation appeared in hairiness of plants subjected to increased exposure along a slope (Bright, 1928), but the hairy covering of certain *Quercus* species becomes thicker upon exposure to greater light intensity (Brenner, 1904). Being chiefly on the stomata-bearing surface, most trichomes apparently do not function in decreasing light intensity (Wiegand, 1910). Certain leaves deprived of trichomes may become 37.5 percent warmer than

normal leaves (Baumert, 1907). A woolly covering which decreases light intensity and transpiration may result in a looser arrangement of chlorenchyma (Clements, E., 1905). Upon removal of felt from *Stachys lanata* transpiration increases 20–50 percent (Yapp, 1912), trichomes of this species retarding water loss, particularly in sunlight (Haberlandt, 1928). Removal of hair from mullen leaves, however, does not alter their resistance to water loss in still air and light, transpiration from internal surfaces amounting to 20 to 40 times as much as through the cuticle (Sayre, 1919). Living trichomes on fern stems markedly increase transpiration (Goebeler, 1886). Trichomes and a waxy covering have little value in reducing transpiration so long as stomata are open, but when stomata close these modifications appear to be protective (Weaver and Clements, 1929).

The known values of trichomes are few in comparison to their abundant development. Gland cells of oriental tobacco leaves contain plastids which enable them to synthesize exudate in situ and eventually to excrete it (Bentley and Wolf, 1945). In certain varieties of *Saccharum spontaneum* spiny trichomes around sunken stomata on the lower leaf surface are associated with a varietal resistance to mosaic, since wherever these trichomes occur, plant lice vectors do not have access to the stomata (Artschwager, 1940). Stomata also occur on the upper leaf surface, however, where they are not similarly protected (Artschwager, 1940).

Trichomes are inferior to a cutinous coat in reducing transpiration (Yapp, 1912), except in strong sunlight where cuticle has less protective value (Wiegand, 1910). Hairy and cutinized individuals of the same species often occur side by side, making the effect of environmental factors questionable (Wiegand, 1910). Plants in the Arctic, subjected to extreme physiological dryness, are covered with cuticle instead of trichomes (Kerner and Oliver). Cuticular transpiration, amounting to ten percent of the total in mesophytes, is practically nil in xerophytes (Weaver and Clements, 1929).

In any single species the value of trichomes probably varies according to whether they are living and transpiring or dead, forming a protective layer. Possibly trichomes are symptoms of excessive water loss rather than structures which function in minimizing it.

ABSORBING HAIRS

At high humidities certain leaves absorb rather than lose water (Thut, 1938). The leaves of more than 100 genera have been described by different investigators as capable of absorbing water (Williams, 1932). Absorption may occur through trichomes and sometimes through hydathodes which ordinarily function in secretion (Haberlandt, 1928). A cellular filament or spreading bristle with stratified cellulose walls often terminates below in a non-cutinized bulbous base with pitted walls and a dense protoplasmic layer. Adjoining subepidermal cells may be radially elongate and colorless, constituting localized water-storage tissue (Haberlandt, 1928). Since water-absorbing trichomes are usually covered by a cuticle insoluble in sulfuric acid, it is probable that their protoplasts function actively in absorption (Haberlandt, 1928). The enlarged one-celled basal portion of an absorbing hair may extend down into photosynthetic or water-storage tissue (Volkens, 1887). Water absorption by submerged leaves or parts of leaves is often sufficient to supply other leaves or leaf parts exposed to air for considerable periods of time (Williams, 1932).

During the dry season many plants on the Egypto-Arabian desert live exclusively on the dew deposited at night on their leaves (Volkens, 1887). Leaf absorption in *Chamaedaphne*, an evergreen ericad, sometimes amounts to three to four times as much as transpiration on a cold winter day, important in decreasing demands upon the root and conducting system at a time when the ground is solidly frozen (Gates, 1914). Certain mesophytes also absorb water through leaves and nodes. Most samples tested in 15 genera, 35 species and 51 horticultural varieties of fruit seedlings regained turgidity and some or all of the weight lost in wilting when immersed in water for two-hour periods (Brierley, 1935).

Absorbing hairs, however, are especially characteristic of desert plants and certain epiphytes (Spalding, 1906). Of those which are most xeric, some absorb water through trichomes and nodes, while others do not (Spalding, 1906). A series of experiments gave evidence of utilization of the foliar absorbed water (Zamfirescu, 1931). Water absorption by leaves might assume some ecological significance, but is not necessarily a useful adaptation (Haberlandt, 1928). Since in wilting plants of temperate climates dew can supply not more than five to ten percent and under or-

dinary conditions not more than one to two percent of the daily water expenditure, absorption by aerial organs plays no role in the general water supply of these plants (Wetzel, 1924). Moistening the leaf surface during the day increases the intensity of transpiration and may have an injurious effect.

Trichomes may also check absorption through leaves. In leathery leaves the strong cuticle offers resistance to absorption proportional to that against cuticular transpiration. Absorption is more rapid where the deficiency in turgor is greatest (Krause, 1935).

Dead spines of *Echinocactus* absorb water from a near-saturated atmosphere, but have no effect on succulence because heavy-walled tissues at the spine bases do not function in absorption (MacDougal, 1912). Water absorbed by loose bark of *Fouquieria splendens* is passed into living stem tissue, resulting in the unfolding of new leaves (Lloyd, 1912).

WATER STORAGE TISSUE

Water storage tissue may develop in the central portion of the xeromorphic leaf (Fig. 6). These enlarged living parenchyma cells have a large vacuole and a peripheral layer of cytoplasm in which a nucleus and a few chloroplasts are embedded (Haberlandt, 1928). Water tissues are the first to show evidence of wilting, their water being withdrawn by photosynthetic cells having higher osmotic pressure. As the water supply is depleted, storage cells contract and then collapse, their radial walls being thrown into folds (Fig. 7). The unthickened condition of radial walls permits this adjustment. When supplied with water the contracted cells recover rapidly, even after repeated depletion (Schimper, 1903; Westermaier, 1872). Under stress, water storage tissue bridges the gap where absorption lags behind transpiration, averting injury to chlorenchyma and preventing temporary interruption of photosynthesis (Haberlandt, 1928). Probably the same environmental influences are responsible for water storage tissue formation in xerophytes as in succulents.

The formation of water storage tissue may be related to production of organic acids, from the influence of limited gas exchange on metabolism or from excess chlorides in soil water (Delf, 1912). More recent evidence indicates, however, that formation of acid

in succulents cannot be attributed to an inadequate oxygen supply to the tissues (Evans, 1932). In late stages of starvation of *Kleinia articulata*, a succulent composite, the pH rises to between eight and nine, which may mark cessation of respiration in the pith, respiratory CO_2 having previously maintained a pH not above six (Thoday and Jones, 1939). In excised barley roots

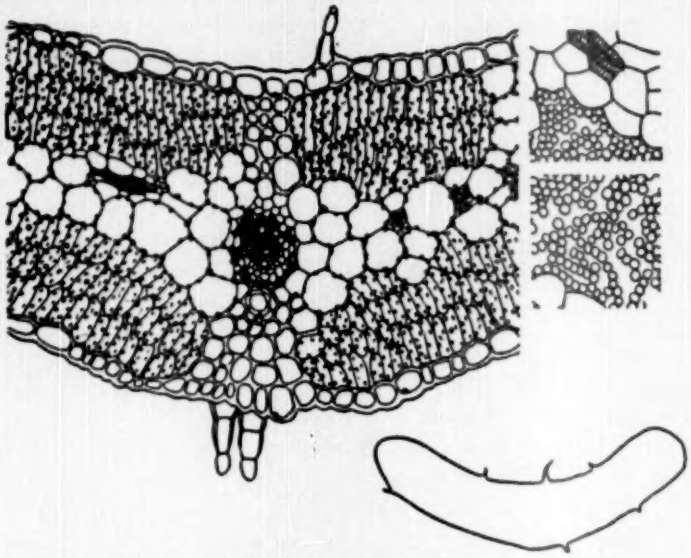


FIG. 6. Central water storage tissue in a xeromorphic leaf (Shields, 1951).

containing an ample supply of available sugar, organic acids disappear when an excess of anions over cations is absorbed and form when cations are absorbed in excess (Ulrich, 1942). The respiratory quotients increase as acids disappear and decrease when acids form, but neither temperature nor oxygen affects ionic balance (Ulrich, 1942).

As a result of water tissue enlargement, old yellow leaves of mangrove are twice as thick as those that have just reached full size (Haberlandt, 1928). Old leaves are reservoirs upon which younger leaves draw for water (Schimper, 1903).

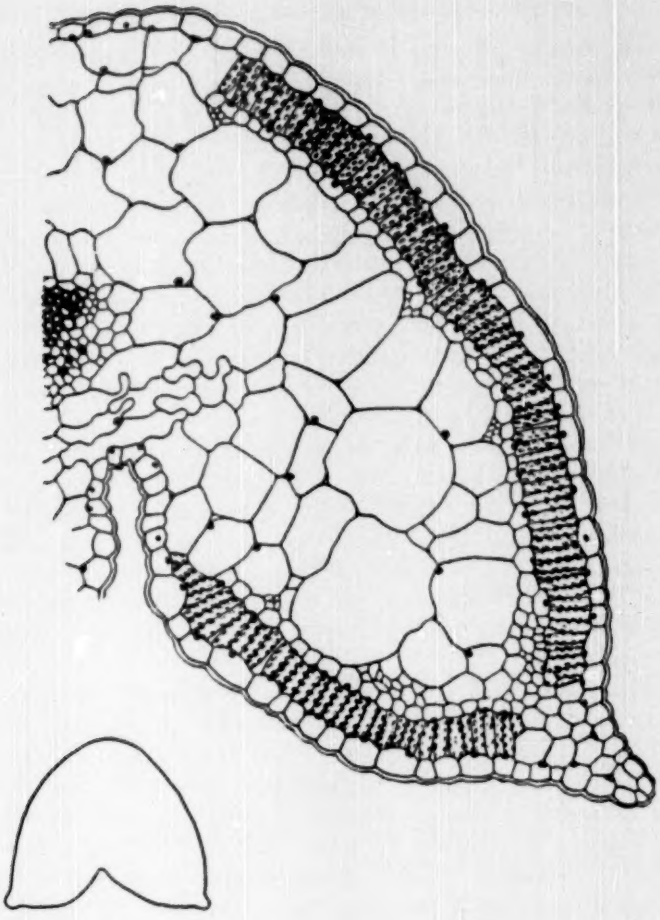


FIG. 7. Showing the collapsed condition of certain central water storage cells during wilting of a succulent-xeromorphic type of leaf (Shields, 1951).

EXPLANATION OF SURVIVAL IN XEROPHYTES

The teleological point of view assumes that the plant in a dry environment must make economical use of water. Most xerophytes are not structurally adapted for reducing transpiration (Maximov, 1931). Many xeromorphic plants peculiar to moist habitats have little drought resistance (Maximov, 1929). The effective adaptation of *Larrea tridentata* to water shortage is the ability of its protoplasm to endure desiccation without permanent injury (Ashby, 1932). The drought resistance develops as a result of a limited water supply at a critical and early stage in leaf development, in some cases before emerging from the bud. A limited water supply, high light intensity, or a nitrogen deficiency result in structural modifications, particularly a greater internally exposed area of palisade (Turrell, 1936), some of which favor excessive water loss. Under a water deficit, conversion of starch to simple carbohydrate and accumulation of photosynthate increase osmotic pressure. It is the effect of high osmotic concentration in decreasing permeability of plant cells that reduces transpiration (Boon-Long, 1941). Plants undergo changes during the day which modify transpiration, and under conditions favoring high evaporation do not respond wholly as free evaporating systems (Briggs, 1916).

Winter hardening of conifer leaves, physiologically comparable to xerophytism, may be through conversion of starch to sugars and oils (Weaver and Mogensen, 1919) and the protective action which sugars exert against precipitation of proteins (Meyer, 1928). The difference in osmotic pressure of evergreen leaves in winter and summer is not great (Meyer, 1928) and may be higher in summer (Stanfield, 1932). When osmotic concentrations are increased by lowering the temperature, hardened cabbage tissue transpires more rapidly than unhardened, hardening having made tissues more permeable (Boon-Long, 1941).

In *Vitis vinifera* and *Rheum rhaponticum* leaves the ratio of protein to soluble nitrogen increases when leaf water content falls. Diurnal fluctuations in this ratio are correlated with changes in pH, acidity increasing with protein (Newby and Pearsall, 1930). In plants abundantly supplied with nitrates, amino acids accumulate, reducing acid production (Pearsall and Ewing, 1929). Both the high amino acid content and the higher pH value allow greater

swelling of protoplasmic colloids, resulting in a higher water content and reduced transpiration (Pearsall and Ewing, 1929). In general low water supply and high temperature are associated with increased polysaccharides, decreased monosaccharides and increased pentosans (Spoehr, 1919). No relation was found, however, between pentosan content of coniferous leaves and either hardiness or rate of dehydration of plant tissue (Doyle and Clinch, 1926).

Echinocactus, a succulent, in diffuse light may lose as much as 2/1000 of its weight in one day immediately after excision of its root system; the same plant six years later under equivalent conditions, except that its weight has been reduced by approximately one-third, loses not more than 1/17,000 of its weight per day (MacDougal, Long and Brown, 1913). This physiological xerophytism has been attributed to the conversion of polysaccharides into anhydrides or wall material, both transformations being induced by a depleted water supply (MacDougal and Spoehr, 1918). The factors which decrease cell permeability, however, reduce transpiration most (Boon-Long, 1941). During desiccation and starvation of cacti, respiration contributes to maintaining a water balance, 0.6 gram of water being formed for each gram of sugar burned (Spoehr, 1919).

In xerophytes there are two opposing modifications: physiologically, a high osmotic pressure, resulting in part from water loss, which produces an internal resistance to flow through decreasing cell permeability; and, morphologically, a palisade type of mesophyll, its formation induced in part by internal resistance to flow, which decreases this internal resistance to a minimum compatible with development of a stem or leaf of a given size and type.

Aridity, universally accepted as an evolutionary factor in the derivation of land plants, must also be a factor in the development of desert forms (MacDougal and Spoehr, 1918), but some of their structural characteristics appear to be incidental. Certain anatomical modifications are apparently symptoms of the changed metabolism which enables the plant to withstand water shortage, but have no survival value in themselves. Leaves from the south periphery of *Ulmus americana*, having more palisade tissue, greater structural compactness and thicker cuticle than those within the

crown, lose approximately 12 times as much water (Hanson, 1917). Evaporation is one and one-half to two and one-third times as great at the south periphery as within the crown (Hanson, 1917). The correlation between xeromorphic structure and high transpiration may be explained in part by the high ratio of internal to external surface associated with the palisade type of mesophyll in xeromorphic leaves (Turrell, 1936). Stomata of xerophytes remain open longer than in mesophytes under the same conditions (Weaver and Clements, 1929). The water deficit in wilted xeromorphic leaves greatly exceeds that in wilted leaves of mesophytes (Maximov and Maximov, 1924). Drought resistance is measured by the capacity to endure water loss rather than by the rate of transpiration when the water supply is inadequate (Maximov and Maximov, 1924). Xeromorphic leaves may lose half their water content without apparent injury (Maximov and Maximov, 1924). The daily deficit in sunflower amounts to 28 percent, while that of the heliophobous plant, *Impatiens parviflora*, is 13 percent (Maximov and Maximov, 1924). Visible loss of turgescence may occur in shade mesophytes when the decrease in water content is so insignificant that it can be measured only with difficulty (Maximov and Maximov, 1924).

No direct correlation exists between drought resistance and the water requirement of plants, xeromorphic leaves being spendthrifts where water loss is concerned. Survival depends upon the ability to withstand desiccation without permanent injury (Maximov, 1931). This resistance develops as a result of purely physical conditions in the plant and soil (Emerson, 1947), and is explained on the basis of changes within the cells, such as increase in osmotic pressure, decrease in cell permeability, and modifications in the protoplasm which increase its water-holding capacity. Structural changes which may or may not further effect the conservation of water are merely the manifestations of these more fundamental physiological changes (Maximov, 1929).

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Chlorophyll	S. Aronoff *Iowa State College*
Physiological Characteristics of Plants in Relation to Drought	K. N. Lal and O. N. Mehrotra *Benares Hindu University*
Movement of Assimilates, Viruses, Growth Regulators and Chemical Indicators in Plants	A. S. Crafts *University of California*
American Coal Ball Floras	Henry N. Andrews *Washington University*
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